

BIOLOGY AND IMMATURE STAGES OF
ANTICHAETA BOREALIS (DIPTERA: SCIOMYZIDAE),
A PREDATOR OF SNAIL EGGS

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Abstract.—Larvae of all investigated species of *Antichaeta* feed on snail eggs. Females of the North American *A. borealis* Foote oviposit directly onto egg masses of the snail *Oxyloma* sp., and all three larval instars feed solely on the eggs. The mature larva usually leaves the egg mass before forming a puparium. *Antichaeta borealis* is multivoltine in northeastern Ohio. Three species of Ichneumonidae, *Phygadeuon* sp. A, *Phygadeuon* sp. B and *Mesoleptus* sp., were reared from puparia collected in the study area. The egg, three larval instars and puparium are described and illustrated. The life histories of the reared species of *Antichaeta* are reviewed and compared.

The genus *Antichaeta* is one of the smaller genera in the family Sciomyzidae, consisting of 5 Palearctic and 8 Nearctic species. An undescribed species is known from Michoacan, Mexico (K. Valley, personal communication). Biological information is available for 7 of the 13 described species. Investigations of the biology and immature stages of *Antichaeta* species were conducted by Fisher and Orth (1964), Knutson (1966) and Knutson and Abercrombie (1977). Larvae of all investigated species feed on eggs of snails.

This paper outlines the life history and describes the immature stages of *A. borealis* Foote, a widespread North American species whose larvae attack eggs of terrestrial snails of the genus *Oxyloma* (Succineidae). Specific morphological features of the immature stages are illustrated in detail. Laboratory rearings and observations reported here are based on material collected during the spring and summer of 1965 at an extensive marsh located about 6 kilometers east of Kent, Ohio.

Biology of *Antichaeta borealis*

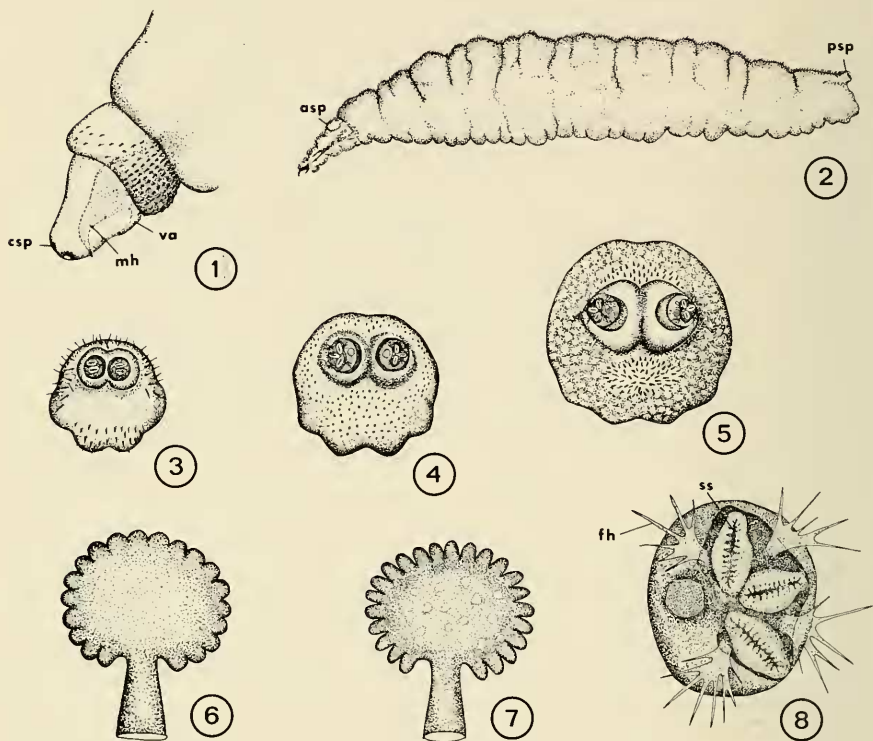
In northeastern Ohio, the only area where the biology was studied, adults and larvae were found most commonly in open, permanent marshes and frequently along the shaded borders of such areas. The habitat distribution of the fly is similar to that of the principal food snail, *Oxyloma* sp.

Recently emerged females of *A. borealis* had a pre mating period (from emergence to first copulation) of 24-36 hours. No specific courtship behavior was observed before mating. The mating position was similar to that of other species of the genus (Fisher and Orth, 1964; Knutson, 1966).

The male was situated dorsally and faced in the same direction as the female, with the anterior portion of his head (not including the antennae) extending to about the mid-length of the thorax of the female. The male's front tarsal segments were laid along her parafrontal areas, laterad to the fronto-orbital bristles and bending them slightly inward. The tarsi extended over the female's fronto-facial ridge, just laterad to her antennae. His middle legs remained free or occasionally rested on the basicostal margins of the female's half-outstretched wings. The hind tarsi of the male were placed on the abdomen of the female. Copulation was not restricted to any particular part of the day, and often lasted an hour. Adults mated frequently before and after oviposition.

Egg masses of *Oxyloma* sp. (probably *O. retusa* (Lea)) apparently provide the only natural oviposition site for *A. borealis*. Although laboratory-reared females also readily oviposited onto egg masses of *Physa* sp., *Helisoma* sp., *Catinella vagans* (Pilsbry) and other species of *Oxyloma*, they did not lay eggs on living or dead snails; and they oviposited on vegetation only when egg masses were not available. Females confined with males had a pre-oviposition period of 3-4 days. Before laying eggs, females exhibited a curious behavior that apparently was a prerequisite for oviposition. They first searched the bottom of the breeding jar for a suitable oviposition site (i.e., snail egg masses). Upon locating a mass, the female would walk onto it and spend several minutes exploring its surface with her front tarsi. After this brief routine she would begin laying eggs. Eggs were scattered over the surface of the masses, with 1-30 eggs deposited on each egg mass in the laboratory. Eggs deposited on *Oxyloma* sp. egg masses were so oriented that the upturned anterior and posterior ends projected above the surface of the egg mass. Soon after the eggs were laid they appeared to be encircled by a colorless liquid which gave the appearance of a small halo around each egg. Eggs that were placed onto egg masses of other snail species did not show this phenomenon. Several females each laid over 150 eggs within 40 days, and one adult deposited 207 eggs within a 35-day period. Hatching occurred within 24-36 hours.

After hatching, each first-stage larva penetrated the egg mass and began attacking the contained eggs. Because of the viscosity of the gelatinous matrix surrounding *Oxyloma* eggs and the position of the eggs within the matrix, it was necessary for the larva to expend considerable energy and time in locating individual eggs. The larva traveled through the matrix in an undulatory manner. After a larva located an egg it began rasping at the vitelline membrane with its mouthhooks. After puncturing the membrane, the larva extended its anterior end into the egg and began feeding on the developing snail embryo. First-stage larvae occasionally entered the egg cell completely, in the process of ingesting its contents. A larva consumed the contents of one egg in a few hours then crawled through the



Figs. 1-8. *Antichaeta borealis*, immature stages. 1. Anterior segments, third-stage larva; 2. Lateral view, third-stage larva; 3. Posterior spiracular disc, posterior view, first-stage larva; 4. Posterior spiracular disc, posterior view, second-stage larva; 5. Posterior spiracular disc, posterior view, third-stage larva; 6. Anterior spiracle, second-stage larva; 7. Anterior spiracle, third-stage larva; 8. Posterior spiracular plate, third-stage larva. Abbreviations: asp, anterior spiracle; csp, sclerotized sensillum; fh, float hair; mh, mouthhook; psp, posterior spiracle; ss, spiracular slit; va, ventral arch.

gelatinous matrix in search of other eggs. During this search for eggs and also during feeding, the posterior spiracles of the first-stage larva were frequently out of contact with the ambient air. The first stadium lasted 3-4 days, and by the 3rd day the larva had developed to such a size that the posterior spiracles could be extended above the surface of the egg mass. First-stage larvae in *Oxyloma* egg masses each consumed from 4-7 eggs. Molting took place within the egg mass.

First-stage larvae developing in *Physa* sp. and *Helisoma* sp. egg masses exhibited, for the most part, the same feeding behavior as those utilizing *Oxyloma* egg masses. Larvae in *Helisoma* egg masses fed on the underside of the mass (the side without a hardened protective covering). Relatively

few of the first-stage larvae feeding on *Physa* sp. and *Helisoma* sp. egg masses reached the second instar.

Second-stage larvae remained in the *Oxyloma* egg masses and actively fed on the living snail embryos. Although second instars were restricted primarily to feeding on snail eggs, one larva that had not fed for 24 hours was observed to kill and eat a recently hatched *Oxyloma* snail. When several eggs had been laid on one egg mass and the larvae subsequently became crowded, several left the original egg mass and searched for others. Second-stage larvae fed with the posterior spiracles in contact with the surface of the egg mass. The second stadium lasted 2-3 days. By the 3rd day most of the larvae had acquired a faint red color in their digestive tracts, and their Malpighian tubules were dark maroon. The reddish coloring in the gut persisted during feeding and molting but disappeared when the larva defecated. The number of *Oxyloma* eggs consumed by each second-stage larva varied from 3-11, the usual number being 7. Like the preceding instar, molting took place within the egg mass. Second-stage larvae feeding on *Physa* and *Helisoma* egg masses failed to develop fully and died before the end of the second stadium.

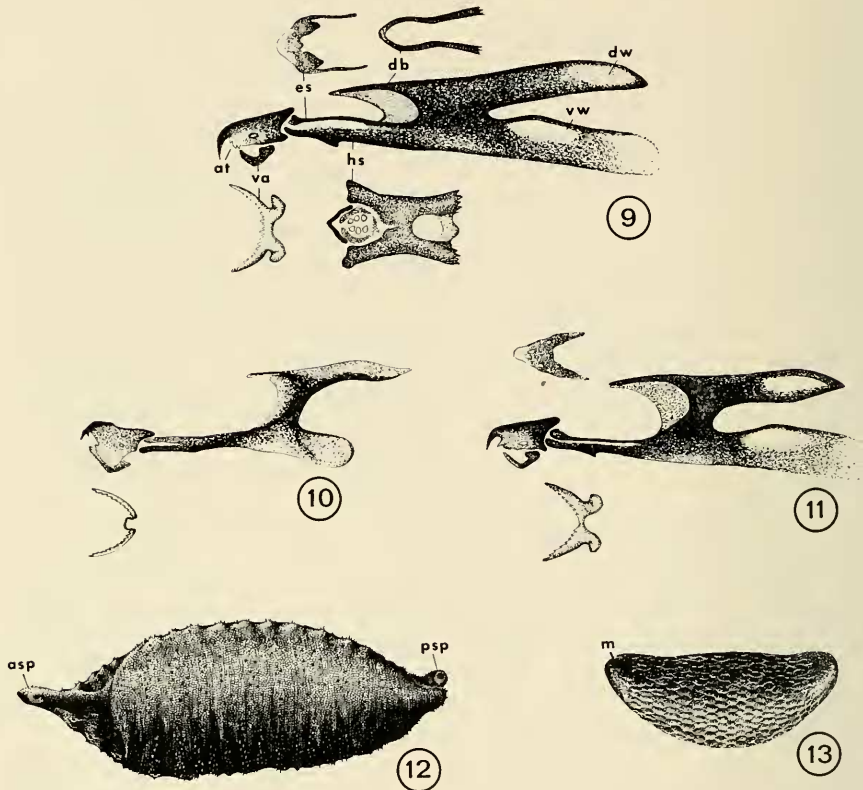
Third-stage larvae continued to feed on eggs within the masses. The reddish color of the intestine and Malpighian tubules became more pronounced, and the tracheal system became dark gray. During the 7-10 days of the third stadium, a larva consumed considerably more eggs than the other 2 instars combined. It was not unusual for a third instar to destroy 105-110 *Oxyloma* eggs.

When third-stage larvae became fully developed, they stopped feeding, frequently abandoned the egg mass and burrowed into the cotton or moist filter paper in the rearing dishes where pupariation occurred. Hardening of the puparium required about 5 hours. The prepupal period lasted approximately 1 day; the pupal period, about 15 days.

The earliest collection record for adults in northeastern Ohio was 16 May (1965); the latest, 10 December (1965). Adult populations peaked around the end of June or the first part of July. Larvae and pupae were discovered in nature between May and September. *Antichaeta borealis* is multivoltine and overwinters as diapausing pupae. In northeastern Ohio first-generation adults emerged in early May.

Puparia collected in January (1966) and retained at temperatures between 5-7°C for at least 60 days produced adults after 8-10 days after being returned to room temperature. Adult males were usually the first to emerge and were followed by females in 24-48 hours. Reared adults lived 7-44 days. Field collected adults lived 3-36 days in the laboratory.

Three species of Ichneumonidae, *Phygadeuon* sp. A, *Phygadeuon* sp. B and *Mesoleptus* sp. (determined by Dr. William Mason) were reared from puparia collected in marshes near Kent. Each infested puparium produced only 1 wasp.



Figs. 9-13. *Antichaeta borealis*, immature stages. 9. Cephalopharyngeal skeleton, third-stage larva; 10. Cephalopharyngeal skeleton, first-stage larva; 11. Cephalopharyngeal skeleton, second-stage larva; 12. Lateral view, puparium; 13. Lateral view, egg. Abbreviations: asp, anterior spiracle; at, accessory teeth; db, dorsal bridge; dw, dorsal window; es, epistomal sclerite; hs, hypostomal sclerite; m, micropyle; psp, posterior spiracle; va, ventral arch; vw, ventral window.

Description of Immature Stages

Egg (Fig. 13).—Length 0.62–0.71 mm, greatest width 0.21–0.24 mm. White. Elongate-ovoid, ventral surface more curved than dorsal surface. Micropylar end slightly truncate (in dorsal view), posterior end rounded. Contents of egg white, developing embryo yellowish white. Chorion distinctly reticulated, with 4- to 7-sided cells. Posterior end without reticulations.

First-stage larva (Figs. 3, 10).—Length 1.10–2.16 mm, greatest width 0.32–0.51 mm. Translucent. Integument slightly papillose, not pubescent. Metapneustic. Posterior spiracular disc (Fig. 3) at apex of elongate postanal portion of segment 12; disc with 2 pairs of weak, rounded lobes (ventro-

lateral lobes slightly larger than ventrals) and 2 spiracular plates, each with 2 spiracular slits. Postoral spine patch reduced to a few rows of dark spinules around anterior margin of segment. Dorsal patches on segments 6–11 reduced to few scattered spinules. Ventrals of segments 6–11 with a few dark spinules on anterior creeping welt; middle and posterior creeping welts with patch of dark spinules, 4–6 spinules wide; spinules few or lacking laterally. Anterior portion of segment 12 ringlike, bearing continuous band of dark spinules; postanal portion greatly extended dorsally. Perianal pad transverse, lobes enlarged. Cephalopharyngeal skeleton (Fig. 10) lightly pigmented, length 0.18–0.23 mm, indentation index approximately 66. Mouthhooks lightly pigmented, triangular with 2 small openings dorsally; darkly pigmented bifid hooks on anterodorsal margin; no accessory teeth. Ventral arch (Fig. 10) curved with 14–16 teeth. Cornua of pharyngeal sclerite without distinct openings; dorsal cornu $\frac{1}{3}$ longer than ventral cornu. (Based on 10 larvae.)

Second-stage larva (Figs. 4, 6, 11).—Length 1.87–2.74 mm, greatest width 0.58–0.74 mm. Unicolorous white. Integument papillose, slightly pubescent. Anterior spiracles (Fig. 6) rounded, with 20–23 marginal papillae; papillae close together and not as elongate as those of 3rd instar. Posterior spiracular disc (Fig. 4) bearing 2 spiracular plates each with 3 spiracular slits and 4 branching, hairlike, interspiracular processes. Spinule distribution similar to that of 1st instar. Sparse patch of dark spinules on anterior creeping welt on venters of segments 6–11 reduced to small patch along meson. Cephalopharyngeal skeleton (Fig. 11) pigmented, length 0.31–0.46 mm, indentation index approximately 55. Mouthhooks deeply pigmented, each with single, lightly pigmented accessory tooth. Ventral arch with winged process laterally; anterior margin with 16–18 variously sized teeth. Ventral cornua slightly longer than dorsal cornua, both with unpigmented windows posteriorly. (Based on 10 larvae.)

Third-stage larva (Figs. 1, 2, 5, 7, 8, 9).—Length 3.60–5.51 mm, greatest width 0.77–1.10 mm. Yellowish tan. Integument papillose, appearing pubescent due to dense covering of small, 0.04–0.06 mm spinules. Body elongate, subcylindrical, tapering anteriorly, somewhat truncate posteriorly. Segment 1 weakly bilobed apically (in dorsal view), each lobe bearing lightly sclerotized sensillum (csp) anterodorsally; postoral segment bearing spine patch posteriorly, with band extending halfway-up on each side of segment (Fig. 1). Anterior spiracles tan, (Fig. 7) dorsolateral on posterior margin of segment 2, subcircular with 22–23 marginal papillae; outer lateral surface of each papilla with small, irregular, clear area. Posterior spiracles at tip of elongate stigmatic tubes on posterior spiracular disc. Spiracular disc (Fig. 5) with 2 pairs of weak lobes; ventrolateral lobes somewhat larger than ventrals; 2 spiracular plates (Fig. 8), each with 3 elongate spiracular slits and dark stigmatic scar; 4 transparent, branched interspiracular

processes or float hairs on each plate. Segments 3–11 with numerous transparent spinules; segments 1 and 2 without spinules. Each segment (3–11) divided ventrally and dorsally by secondary integumentary folds to form anterior, middle and posterior welts. Segment 3 with row of dark spinules on anterodorsal margin, venter of segment with sparse spinule band anteriorly. Segment 4 without dark spinules dorsally; venter of segment with sparse spinule band, 3–4 spinules wide, on anterior margin. Segments 5–6 with band of a few dark spinules on anterior and middle welts. Segments 6–11 without distinct dark spinules dorsally or ventrally. Segment 12 with a few pre-anal spinules, located along meson. Perianal pad bilobed, anus longitudinal on mid-line. Cephalopharyngeal skeleton (Fig. 9) deeply pigmented, length 0.77–0.79 mm, indentation index approximately 51. Mouthhooks (in dorsal view) converging anteriorly, separated posteriorly; 3 lightly pigmented accessory teeth (at) beneath each hook part. Anterior margin of ventral arch (va) with 22–23 anteriorly directed, variously sized teeth. Epistomal sclerite (es) fused to parastomal bars of pharyngeal sclerite. Pharyngeal sclerite with dorsal and ventral cornu separated by sinus extending slightly more than halfway to anterior edge of sclerite, ventral cornua with elongate window (vw), dorsal cornua with small, tapering window (dv); narrow parastomal bars arising from anterior margin of sclerite. (Based on 10 larvae.)

Puparium (Fig. 12).—Length 3.71–4.82 mm, greatest width 1.70–2.12 mm. Dark brown. Elongate, subcylindrical, anterior end flattened dorso-ventrally, posterior end tapered. Ventral surface slightly more flattened than dorsal. Integument dull, opaque, with pubescent appearance due to tanned spinules of 3rd instar. Intersegmental and secondary intrasegmental folds distinct. Segment 1 invaginated. Anterior spiracles (asp) tan, fan-shaped. Postanal portion of segment 12 narrower than pre-anal portion: Perianal pad bare; lobes on posterior spiracular disc reduced; stigmatic tubes uplifted and divergent; spiracular plates yellow. (Based on 10 puparia.)

Discussion

Information available on the studied species of *Antichaeta* indicates that the species segregate primarily by habitat and species of food utilized. In North America, *A. testacea* Melander and *A. borealis* are commonly found in permanent marshes and are associated with snails that produce eggs more or less continuously throughout the year. Both of these species of *Antichaeta* are multivoltine. The habitats of *A. melanosoma* Melander are vernal pools, temporary woodland pools and areas in large marshes where there is a seasonal drop in water level. In such habitats the host snail, *Aplexa hypnorum* (L.), is most active at 1 or 2 times a year. As might be expected, this species is univoltine (Knutson and Abercrombie, 1977).

The 4 European species, *A. analis* (Meigen), *A. atriseta* (Loew), *A. obliquosa* Enderlein and *A. brevipennis* (Zetterstedt), all seem to be associated with vernal marshes (Knutson, 1966).

A wide variety of foods is utilized by different *Antichaeta* species. According to Fisher and Orth (1964), first- and second-stage larvae of *A. testacea* can feed on the eggs of several snail species, including those of *Oxyloma*, *Physa*, *Succinea*, *Radix*, *Stagnicola*, *Pseudosuccinea* and *Helisoma*. Third-stage larvae continue to feed on snail eggs but also can kill and eat juvenile and adult snails. Larvae of *A. testacea* show the most generalized feeding habits of all the studied species of *Antichaeta*. In the laboratory, first- and second-stage larvae of *A. melanosoma* and *A. borealis* feed on the eggs of several species of snails, but unlike *A. testacea*, the larvae failed to continue development on eggs other than those of the host species. Third-stage larvae of *A. melanosoma* killed and ate adult snails of the host species (Knutson and Abercrombie, 1977), but third-stage *A. borealis* larvae limited their feeding to *Oxyloma* eggs and refused juvenile or adult snails. Under laboratory conditions larvae of *A. analis* and *A. brevipennis* fed on eggs of *Lymnaea* and *Succinea* snails, but neither attacked juvenile or adult snails.

In areas where species overlap in habitat distribution, they are segregated by differential food utilization. For example, in northeastern Ohio, 3 species of *Antichaeta*, *A. borealis*, *A. fulva* Steyskal, and *A. melanosoma*, occur in the same marsh habitats at approximately the same time of year (late April-June). The first species utilizes *Oxyloma* eggs; the second, *Lymnaea* sp. eggs; and the third, eggs of *Aplexa* and *Physa*. There may be some slight habitat segregation (especially with *A. melanosoma*) among the 3 species, but it does not seem to be as significant an isolating factor as the differences in food utilization.

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